Anti-predatory responses of white rhinoceros (*Ceratotherium simum*) to simulated risk. Does poaching create a landscape of fear?

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Abstract

Predators affect prey's behaviour which can lead preys to change their spatial use of the habitat, creating a landscape of fear. This is not generally the case for white rhinoceros (*Ceratotherium simum*), which as megaherbivores (<1000 kg) are relatively invulnerable to non-human predators. However, due to poaching, rhinos are exposed to a human predation pressure, which would be expected to create a landscape of fear. It is uncertain if rhinos recognize human predator and, if they do, it is unknown whether they exhibit successful anti-predator responses to human predation risk or not. In this study, I conducted a landscape-scale playback experiment testing if rhinos exhibited different anti-predator responses when they were exposed to non-threatening sounds (i.e. control sounds) and several threatening sounds (i.e. lion, human voices and gunshots). I evaluated whether rhino showed anti-predator responses to different simulated risk sounds. In addition, I tested whether rhino anti-predator responses to those sounds were stronger in high poaching intensity areas. The experiment showed that rhinos ran from all sounds that simulated risk, responded defensively from gunshot and lion sounds and increased vigilance for human voices and lion sounds. However, the strength of their responses did not increase with poaching intensity. The results of this study could be useful for implementing management anti-poaching strategies in the future.

Keywords: White rhinoceros, poaching, playback experiment, anti-predatory behaviour, landscape of fear, perceived predation risk

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1. Introduction

Predators induce fear in prey species, which respond by changing their behaviour and distribution (Brown et al., 1999). Indirectly, predators trigger a cascading effect through several trophic levels, influencing other species communities and general ecosystem (Ripple et al., 2001). This effect of predators on their prey's behaviour and spatial use patterns can create a landscape of fear (Laundré et al., 2001). In this landscape, an animal's use of an area would vary depending on the perceived predation risk in the habitat, trying to avoid more risky areas in order to reduce its vulnerability to predation (Laundré et al., 2010). However, not all prey species are equally vulnerable to predation. Megaherbivores, species which exceed 1000 kg (Owen-Smith, 1988), are relatively invulnerable to non-human predators (Owen-Smith, 1975). Thus, their populations are limited by food resources (bottom-up) and are generally considered not to be limited by predators (top-down). Despite this, anti-predator responses have been shown in both African and Asian elephant species, using top-predator's vocalizations (MComb et al., 2011, Thuppil & Gross, 2013). Although adult megaherbivores are normally excluded from predators' diet (Owen-Smith and Mills, 2008) their calves can be hunted. In addition, humans have, for millennia, hunted megafauna as a predator (Scott, 1980, Håkansson, 2004) contributing to the extinction of some megaherbivore species during the late Quaternary (Sandom et al., 2014, Bartlett et al., 2016).

In recent times, conservation efforts have isolated megaherbivores in nature reserves for several generations from major human disturbances (Brooks, 2006), including human predation. As a result, megaherbivores have potentially lost their fear of humans and become accustomed to their presence. In this context, megaherbivores could become naïve prey due to their lack of experience with human predators. Naïve prey would fail to exhibit successful anti-predator responses to human predation risk (Berger et al., 2001) to which they may not be accustomed anymore. In ungulate species some studies have shown that they could recognize predator species which are locally extinct in their habitat (Hettena et al., 2014, Dalerum and Belton, 2015) or were able to re-learn their fear of the predator through direct experience (Berger et al., 2001, Berger, 2007). However, it is still uncertain if this is possible for megaherbivores.

Among megaherbivores, in the case of white rhinoceros (*Ceratotherium simum*), human predation pressure led to the near extirpation of the global population at the

end of 19th century (Owen-Smith, 1988) and the recent functionally extinction in the wild of the northern subspecies (*Ceratotherium simum ssp cottoni*). The population of the southern subspecies (*Ceratotherium simum ssp simum*) recovered from an estimated 100 individuals in the first decade of the 20th century to around 20 000 at the beginning of 21st century due to conservation efforts in protected areas (Emslie and Brooks, 1999) However, during the last approximately 10 years, rhinos have been increasingly exposed to human predation pressure again in the form of poaching for their horns. Poaching intensity reached its peak in 2014 and has slowly declined since then due to protection and law enforcement efforts (Emslie, 2020). Despite this decline, poaching activity is still a conservation problem and the main cause for considering white rhinoceros a near-threatened species (Emslie, 2020). In addition, due to the COVID-19 world crisis, several protected areas may experience an increase in poaching activity (Buckley, 2020).

Poaching would be expected to create a landscape of fear (Ihwagi et al., 2019) where rhinos could potentially predict the predation risk in each area and try to avoid areas with higher risk. This could be the case for rhinos if they still perceive predator risk from humans or re-learn to identify it. There are some studies that tested the responses of African elephants to various signs of human odours and sounds (Bates et al., 2007, MComb et al., 2014). These studies showed how elephants adopt different behavioural strategies depending on the level of threat that the stimuli represented. A study focused on rhinos have shown rhino run away from human voices more frequently than from top-predator vocalizations, and gunshots (Zanette and Clinchy, in press). These studies used playback experiments to elicit a fear response by the exposed animals. Playback experiments consist of exposing an animal to the broadcasted sounds and the responses of the focal subject are noted. As another example of a playback experiment with rhinos, Penny et al., (2019) used bees and siren sound treatments in order to explore their suitability to deter rhinos as an anti-poaching strategy. Only the siren treatment was strong enough to make rhinos flee when playbacks were broadcasted.

Here I use playback experiments to assess whether white rhinoceros (henceforth rhinos) exhibited anti-predator responses when they are exposed to sounds that indicate risk. Various threat levels were simulated by using four different playback sounds; a control sounds (birds native to the study area) that we predicted to be non-risky and three risky sounds namely, lions roaring and growling, gunshots and human voices. Bird sounds exemplify non-risky sounds for rhinos, while the other three playbacks sounds represent potential threats to them. Lions might not be a potential threat for adult rhinos but it would be for calves, which could potentially trigger anti-predator responses in adult rhinos. Human associated sounds (gunshots and human voices) represent risky stimuli for rhinos. Therefore, I could expect stronger responses to risky-stimuli compared to control sounds. Anti-predator responses could also vary with group size (Creel et al., 2014). Larger groups would

potentially make rhinos more confident against risky treatments, while solitary individuals would react stronger to them. Additionally, I also investigated whether the strength of rhino's anti-predatory response to humans increased with the risk of poaching. If poaching created a landscape of fear, rhinos in low poaching areas would be more naïve to human predation risk than rhinos in high poaching areas. Naïve rhinos would potentially fail to exhibit effective anti-predator responses to human-associated stimuli.

- I hypothesized that rhinos would have stronger responses to risky playbacks treatments than to control sounds.
- Secondly, I hypothesized that rhinos' response to risky playback treatments would be less pronounced in larger group sizes.
- Finally, I predicted that rhino responses to human associated treatments i.e. human voices and gunshots in the first hypothesis will be stronger in areas where poaching intensity is higher.

2. Methods

2.1. Study area

The study took place in Hluhluwe-iMfolozi Park (hereafter HiP), an approximately 900 km^2 protected area in KwaZulu-Natal province, South Africa. The altitudinal range varies from 45 to 750 meters above sea level (Howison et al., 2017). The study period was during the summer months (October 2019 - January 2020) which corresponds to the wet season, when most annual rainfall occurs. Rainfall varies from 1000 mm in northern areas to 550 mm in the south (Howison et al., 2017). Vegetation structure is quite heterogeneous, from open grasslands to closed woodlands, through park-like savannah woodlands. The park is composed of two main areas, Hluhluwe in the north and iMfolozi in the south which are separated by a national road crossing the park. The southern section of the iMfolozi area is considered the wilderness section, where no manipulations are allowed. The wilderness section was therefore not part of this study (figure 1). Currently, HiP holds a large white rhino population with one of the highest rhino population densities of Africa due to a successful implementation of conservation programs (Linklater and Shrader, 2017). Following local extinction, the park's apex predator, lion (*Panthera leo*), returned to the park in 1965 when an individual walked into the park. Later, several successful lion introductions occurred in the northern areas between 1999 and 2004 (Trinkel *et al.,* 2008). In 2015, the lion population reached an estimated 120 individuals (Somers et al., 2017).

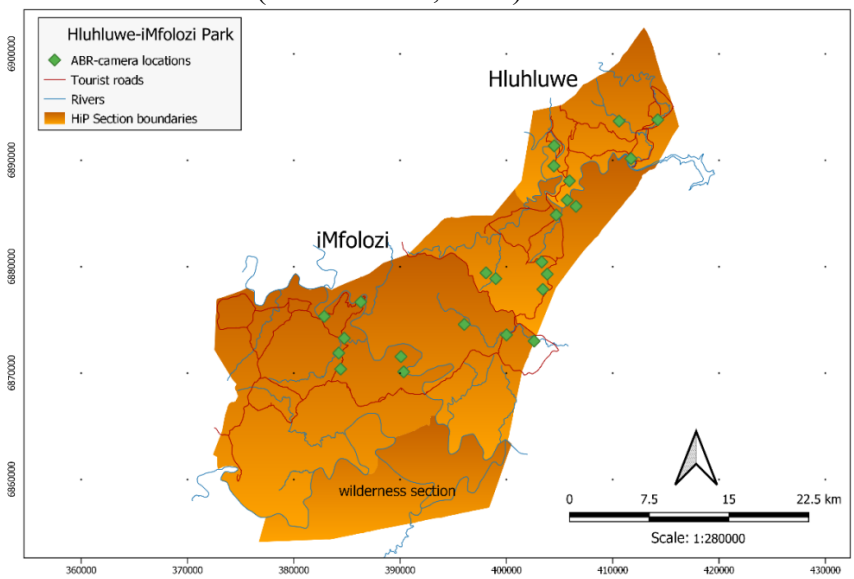

Figure 1. Hluhluwe-iMfolozi Park and the locations of Automated Behavioural Response systems (ABRs). The wilderness section, tourist roads, rivers and boundaries are also indicated.

2.2. ABR and experimental design

I conducted a playback experiment, monitoring rhino behaviours in high and low poaching intensity areas. Between October 2019 and January 2020, I installed automated behavioural response (ABR) systems at 24 different locations. These ABR systems consist of a motion-triggered camera trap connected to a speaker (Suraci et al., 2017a). Thirteen of the 24 locations were in areas with high poaching intensity and 11 were in areas with low poaching intensity (see below for the estimation of poaching intensity). ABR locations were at least 1 km apart. Each ABR was deployed for around two weeks and there were a maximum of 6 ABRs deployed at the same time in the field. I installed each ABR adjacent to a rhino latrine to maximise rhino visitation to ABR sites and to minimise other animal encounters. A rhino latrine is a communal place where rhinos defecate and transmit social information to other rhino through olfactory communication (Marneweck et al., 2017). I secured the ABR to a tree at 1.5 m height, with the focal point of the camera (which usually was the rhino latrine or in some cases the path leading to the rhino latrine) at around 8 m distance from the front of the camera (figure 2). If it was necessary, I cleared any vegetation in front of the camera that could cause false triggers. I placed the speaker 0.5 m above the camera, surrounding it with an aluminium cage for its protection (figure 2). The camera started recording a video when its PIR sensor detected movement and I programmed the speaker to play a 10 seconds vocalization 3 seconds after the video started. This ensured that the treatment sound only started after the individual was already in front of the camera. The cameras were Browning Recon Force Extreme BTC-BFHD-PX and recorded 30 and 20 second videos during day and night (via Infrared LED flash) respectively. Each speaker contained a playlist with 4 different sound treatments, 3 predator-type (risky) sounds and 1 control sound. The playlist was programmed to switch sound treatment every 15 minutes. The predators' playbacks included lion vocalizations (roaring and growling), gunshots and humans speaking. The human voices included a mixture of men and women speaking the three dominant local languages: Zulu, Afrikaans and English. I used local bird sounds as control sounds. I scheduled the bird sounds to play at the appropriate activity period: African hoopoe (*Upupa africana*) for day-light time, fiery-necked nightjar (*Caprimulgus pectoralis*) at twilight and sunrise (15 minutes after and before each event) and African wood owl (*Strix woodfordii*) during the night time (Zanette and Clinchy, in press). I set the average volume of all treatments to 80 dB at 1m and adjusted the volume of the sounds in the field to ensure it was consistent across all treatments.

Figure 2. ABR system set up in the field.

2.3. Ethics Statement

This study required no handling of animals or invasive sampling. The disturbance caused by the vocalization might influence rhinos' behaviour for a few seconds in some cases due to minimum distress after the exposure. The research was approved by the Ethics Committee of Nelson Mandela University, South Africa (Reference Number: A19-SCI-ZOO-007).

The experiment was also approved by the HiP managers and Park ecologist. Additionally, because the treatments included gunshot sounds, I performed a demonstration of the ABR operation system to the reserve managers in order to give more legitimacy, inclusiveness and transparency to the research process.

2.4. Scoring behaviour analysis.

I scored the rhinos' behaviour before and after each sound treatment using the software Solomon Coder (Péter, 2011) for Windows. I registered the behaviours based on recognised rhino behaviours (Owen-Smith, 1975) and following previous playback studies (McComb et al., 2014, Dalerum and Belton, 2015, Clinchy-Zanette et al., 2016, Suraci et al., 2017b, Palmer and Gross, 2018, Zanette and Clinchy, in press). I used the following behaviours to score rhinos' responses:

*Table 1. Behaviours divided in 3 different categories (movement, attention and details). Behaviours listed within a category were mutually exclusive (i.e. only only one could occur at a time). If neccessary, behaviours and details across categories could be specified simultaneously to define each behaviour more especifically e.g. "**Walking**, with **head hanging**, **ears scanning**". Coloured behaviours were used as response variables: yellow for running, green for defensive behaviours, blue shades for low vigilance and high level of vigilance and grey for scanning.*

Category	Behaviour	Behaviour definition
Movement	Standing	The animal is in an upright position and is remaining in one location. The animal can make three or less steps in any direction to scan.
	Walking	The animal took more than three consecutive steps in a single direction which its head not towards the camera. Left and right legs alternate.
	Retreating	The animal took more than three consecutive steps backwards. Left and right legs alternate.
	Running	The animal took more than three consecutive steps in a single direction away from the camera at speed greater than walking. Left and right legs alternate.
	Approaching	The animal took more than three consecutive steps towards the camera with its head also turned towards the camera.
	Wallowing	The animal is lying down in the mud with limited attention of its surroundings.
Attention	Looking at camera	The animal was standing or walking with its head raised up above their knee and looking directly at the camera with both eyes visible.
	Defecating	The animal was standing or walking and defecating. This behaviour started when the first dung bolus came out of the anus and finished when the last dung bolus hits the ground. It also included peeing.
	Head down	The animal was standing, walking or retreating with its head down with the horn touching the ground (almost) in a horizontal position to the ground. Defensive position (Figure 3).
	Head hanging	The animal was standing or walking with its bottom lip below the height of its knees so that its nose is close to or touching the ground. This was considered the low vigilance (Figure 3).
	Head up	The animal was standing with its bottom lip above the height of its knees and below its belly. The head could move for scanning.
	Head horizontal	The animal was standing with its head completely horizontal with the rest of its body and therefore above its belly. The head could move for scanning. This was considered the high vigilance (Figure 3).
Details	Feeding	The animal was standing or walking and grazing or chewing at the same time.
	Slow	The animal was approaching (walking towards) the camera slowly.
	Fast	The animal was approaching (running towards) the camera fast.
	Group	The animals were standing, gathering and putting their backs/bottoms together (Figure 3).
	Ears scanning	The animal scanned around with its ears. The left and right ears alternate.

In every video I scored and recorded the responses for every rhino, so for videos where the number of rhinos was larger than 1, I registered the responses of every single rhino, instead of using the majority response of the group (as opposed to methods in Dalerum and Belton, 2015; see statistical analysis section below for the

selection of independent data points). I decided to quantify individual responses rather than average responses for two main reasons: First, rhino herds are normally smaller than other herbivores such as impala (*Aepyceros melampus*), nyala (*Tragelaphus angasii*) or blue wildebeest (*Connochaetes taurinus*), which lowered the scoring effort required. Secondly, because scoring individual responses allowed for the possibility to produce more detailed results, differentiating the behavioural responses between individuals.

2.5. Poaching index estimation

For every ABR location, I calculated nine poaching intensity scores (henceforth PI). The PI estimates were based on the cumulative number of poaching events within a 1, 2 or 3 km radius and over a 1, 2 or 3 year period (i.e. 9 combinations).

Additionally, I categorized each PI as low or high, using the median values for each PI with the same radius and year period. For example, I calculated the median value for the PI measured for 3 km radius and 3 years period for the 24 locations.

Unfortunately, I am not allowed to reveal PI values because poaching information is sensitive information.

2.6. Statistical analysis

2.6.1. Calculation of independent data points and response variables.

For every video, I noted the group size, sex, age class (adult, sub-adult or calf), the presence of other species in the video, sound treatment (human, gunshot, lion or control), herd ID (definition below) and if it was a first exposure or not. As first exposure, I considered the videos where the time interval between successive videos of the same playback treatment in the same location was larger than 60 minutes (Suraci et al., 2017c). I defined a "sequence" as a series of videos at the same location and in response to the same playback treatment and with a maximum of one minute between consecutive videos (Forrester et al., 2016). In addition, I recorded rhino individuals within each sequence separately. This led to a sample size of n=279 sequences for 501 individuals. I used summarized responses per sequence with both Generalized Linear Models (GLM) and Generalised Linear Mixed Models (GLMM). Therefore, if a rhino stayed for two consecutive videos with the same treatment in front of the camera (same sequence), I calculated a single data point per sequence (table 2). I also calculated sequence length by counting the total number of videos per sequence.

Table 2. Statistical methodology, videos included, rhinos per video and data independence achieved for each analysis.

Analysis	Statistical test	Videos included	Rhinos per video	Data independence achieved
1	GLM	An single response value per 1st exposure sequence (i.e. only sequences where the time interval between successive video sequences of the same playback treatment in the same location was larger than 60 minutes)	1 rhino per video (the individual nearest to the cameras)	Sub setting the data to 1st exposure sequences
2	GLMM	All videos	All individuals	Defining data dependence with random factors in a mixed model

I performed two different analyses on each of five response variables: a generalized linear model (GLM) on a data subset and a generalized linear mixed model (GLMM) on the full data set (table 2). The GLMM is able to handle the dependencies in the dataset (i.e. repeated measures of the same locations and potentially the same herds), however, the GLM was still retained so as to have a comparable methodological approach to a previous similar study (Zanette and Clinchy, in press). To partially achieve data independence in the GLM analysis, I subset data points to only include the 1st exposure video sequences and only a single rhino per video (the individual closest to the camera). However, this sub-setting approach did not fully take care of the repeated measures per location and thus I performed the second GLMM analysis (see below for details on model structure).

I considered rhinos as being part of the same herd when they were recorded in the same location and in successive videos within a time interval of less than 60 minutes, regardless of the playback treatment. For each herd I also noted the herd size, which I defined as the largest group size (total number of rhinos in one video) recorded within all the videos considered to be from the same herd.

A set of response variables were calculated per sequence and used in GLM and GLMM analyses.

I summarised the behaviours in five key behavioural responses variables:

(1) **Ran**, if the rhino ran at any time during the sequence following the start of the sound playback. (Binary response, ran or not).

(2) **Defensive** behaviour, if the rhino displayed any of the following behaviours (grouping, head down, approaching fast or retreating) during the sequence following the start of the sound playback. (Binary response, defensive or not). (See figure 3)

(3) **Vigilance**, as the maximum vigilance score that the rhino reached during the sequence following the start of the sound playback. "Head horizontal" was considered as the highest level of vigilance and "head hanging" considered the lowest. For the analyses I tested low vigilance against high vigilance. (Binary response, low or high vigilance). (See figure 3)

(4) **Scanning**, which was the proportion of time that the rhino spent scanning with their ears during the sequence following the start of the sound playback. (Normal distribution)

(5) **Sequence length**, the total number of videos per sequence. This variable reflected the duration of visits; i.e., how long rhinos stayed in front of the camera. (Normal distribution).

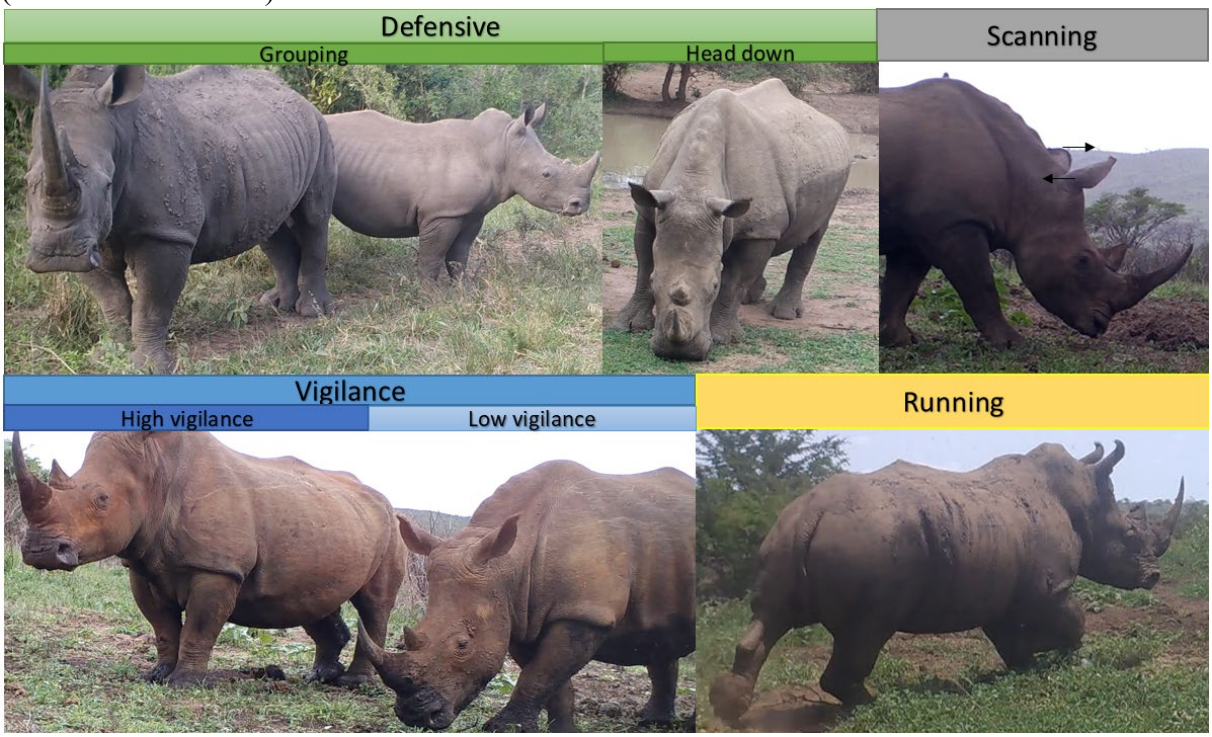

Figure 3. Examples of rhino behaviours for the first four response variables. (From left to right and top and bottom). Defensive: Two rhinos grouping, a rhino with head down. Scanning: the direction of the arrows indicate the movement of the ears. Vigilance: The rhino on the left is high vigilant (Head horizontal) and the one on the right is low vigilant (head hanging) (Note the difference on the head position between head hanging (low vigilance) and head down (defensive). Running: rhino running. All photos were taken from the ABR videos used in this study.

2.6.2. Model reasoning and selection for GLM and GLMM

In order to test previously stated hypotheses, I included PI, treatment and group size as explanatory variables. I expected that rhinos had stronger responses to human associated sounds in high poaching areas and also that they had more moderate responses in larger groups. Consequently, I added the interaction of PI with treatment and group size with treatment (model 1 below) to test if both hypotheses were true. I removed one interaction term at a time to test the contribution of each (model 2 and 3 below). Finally, I added a fourth model (model 4 below) to test if rhinos' responses to risky treatments were stronger compared to control sounds. The responses to control sounds would not be expected to increase with poaching intensity. Therefore, I did not test the effect of poaching intensity for all the treatments combined, i.e. model with only PI as explanatory variable.

For both analyses (GLM and GLMM), I used the five response variables (see section above) in these four different model structures:

(1) PI (continuous/factorial)+Treatment+ Group size (GS)+ PI(continuous/factorial) x Treatment+ Treatment x Group size (GS)

(2) PI (continuous/factorial) +Treatment+ Group size (GS)+ PI (continuous/factorial) x Treatment

(3) PI (continuous/factorial) +Treatment+ Group size (GS)+ Treatment x Group size (GS)

(4) Treatment

I used the full model (model 1 above) to select the PI estimate (of the 9 different estimates, see section 2.5) that provided the best fit and whether it fit best as continuous or factorial variable. Then I continued using that PI value throughout the models simplification/ model comparison.

In addition, I used AIC for model selection. According to Burnham and Anderson (2002), models with 2 or less AIC difference are evenly supported. In these cases, I selected the most parsimonious model i.e. the model with the least amount of parameters. If the models had the same amount of parameters, then I would select the lowest AIC.

Finally, I did not do multiple comparisons among the four playback treatments and I was only interested in comparing risky playback treatments against control sounds in order to test my first hypothesis.

2.6.3. GLM for first exposures sequences.

I ran Generalised Linear Models (GLM) using the "nlme" package (Pinheiro et al., 2020) in R (R Core Team, 2019). The sample size was 210 individual observations (first exposure sequences), except for the models testing the vigilance response which had 142 individual observations because of the rhinos that did not exhibit either low or high vigilance. I kept this statistical test (GLM – first exposures), so I could compare my results with a similar study (Zanette and Clinchy, in press).

2.6.4. GLMM for all sequence responses.

In addition to the GLM analyses, I used GLMM in order to use all the sequence responses for all individuals (n=501), i.e. multiple rhinos per video and not only first exposures. For this purpose I used "lme4" (Bates et al., 2015) and "nlme" R packages to analyse binary and normally distributed response variables respectively. For the vigilance analysis, the sample size was 405 and for the sequence length analysis the sample size was 279 (total number of sequences).

For normally distributed variables I assessed the assumption of homogeneity visually using QQ plots, residual vs fitted plots and histograms of model residuals. I also used the "Bartlett test" and "variance test" to test homogeneity statistically. In case it was needed, I included variance structures using the "weights" function from the nlme package to correct heterogeneity of the residuals.

I included herd ID nested in location as random effects. This minimized autocorrelation from measuring individuals within the same herd and location. Again using AIC, I tested whether the inclusion of herd ID as a random effect was necessary. For all the selected models herd ID as a random effect was included.

3. Results

3.1. Sampling results

Rhinos were recorded in 19 of the 24 locations. Of the five locations where rhinos were not recorded three were from high poaching intensity areas and the other two from low poaching intensity areas. This yielded 1219 data entries (scored rhino individuals x videos). In total 617 white rhino videos were recorded. The videos were equally distributed for each treatment among sequences (table 3).

Table 3. Number of entries per treatment for all the individual entries, all the sequences and first exposure sequences.

	Control	**Gunshot**	**Human**	**Lion**	**Total**
All entries	419	248	267	285	1219
All sequences	67	75	63	74	279
First exposure sequences	52	52	54	52	210

The average group size per video was 2.5 and the maximum was 7, which only occurred on one occasion. I obtained 168 herds and an average herd size of 2.05 individuals.

3.2. Response 1: Ran

3.2.1. GLM

The probability of rhino running or not was best explained by model 4 i.e. the model including the single term for the playback treatment. Although, model 3 (which included the additive effects of group size, treatment and poaching intensity - measured as a continuous variable over a three km radius and a two year period - and the interaction between treatment and group size) had a similar AIC. However, I selected the first model because it included fewer parameters (table 4).

Table 4. Estimate value, standard error, z and p value for each level of explanatory variable from the best model explaining the probability of rhinos running from playback disturbance. Model structures and AIC support for all competing GLM models is shown below the estimates table with the selected model highlighted in grey.

	Estimate	**Std. Error**	**z value**	**Pr(>|z|)**
Intercept	-1.70	0.38	-4.43	<0.001 ***
Playback Gunshot	1.47	0.47	3.10	0.002 **
Playback Human	1.56	0.47	3.30	<0.001 ***
Playback Lion	0.89	0.49	1.83	0.067 .

	Model structure	AIC
Model 1	PI (c/f)+Treatment+ GS+ PI(c/f) x Treatment+ Treatment x GS	268.96
Model 2	PI (c/f) +Treatment+ GS+ PI(c/f) x Treatment	266.62
Model 3	PI (c/f) +Treatment+ GS+ Treatment x GS	264.37
Model 4	**Treatment**	262.80

Rhino were significantly more likely to run in response to gunshot and a human voice sound compared to a control sound (figure 4). Lion vocalization treatment was close to being significantly different from control sound as well (p-value =0.06) (table 4).

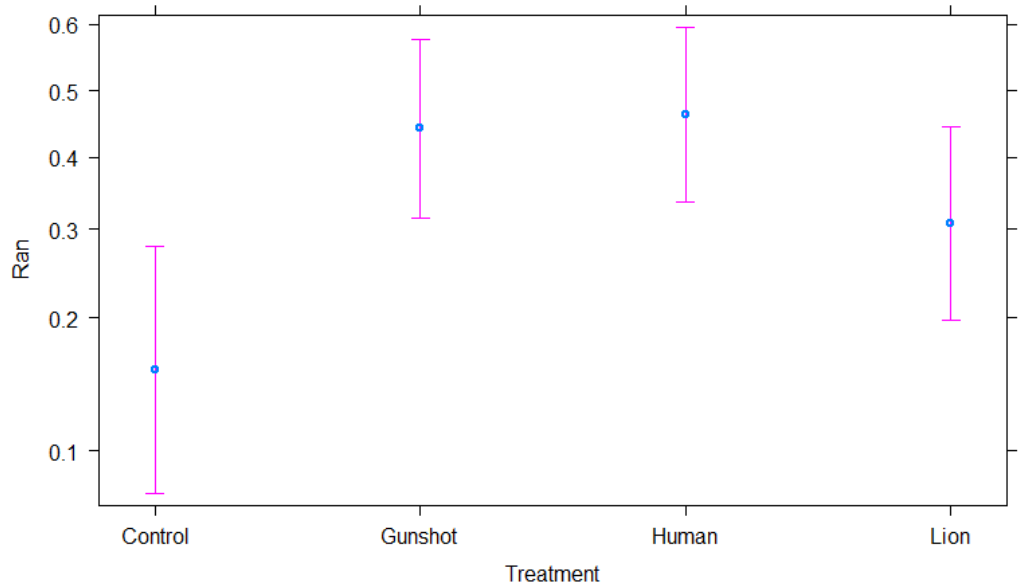

Figure 4. Probability of rhinos running after the playback and 95% confident limits for each playback treatment for GLM analysis.

3.2.2. GLMM

Model 4 (singular effect of treatment) was again the most supported model. Rhinos were more likely to run in response to all risk sound treatments compared to their probability of running during a control sound (table 5). Among risky treatments, the human voices treatment had the highest probability of rhino running compared to control sounds (figure 5).

Table 5. Estimate value, standard error, z and p value for each explanatory variable from the best model explaining the probability of rhinos running for playback disturbance. Model structures and AIC support for all competing GLMM models is shown below the estimates table with the selected model highlighted in grey.

	Estimate	**Std. Error**	**z value**	**Pr(>|z|)**
Intercept	-1.97	0.42	-4.65	<0.001 ***
Playback Gunshot	1.53	0.47	3.25	0.001 **
Playback Human	1.95	0.47	4.13	<0.001 ***
Playback Lion	1.18	0.46	2.57	0.010 *

	Model structure	AIC
Model 1	PI (c/f)+Treatment+ GS+ PI(c/f) x Treatment+ Treatment x GS	577.20
Model 2	PI (c/f) +Treatment+ GS+ PI(c/f) x Treatment	578.40
Model 3	PI (c/f)+Treatment+ GS+ Treatment x GS	577.50
Model 4	**Treatment**	572.99

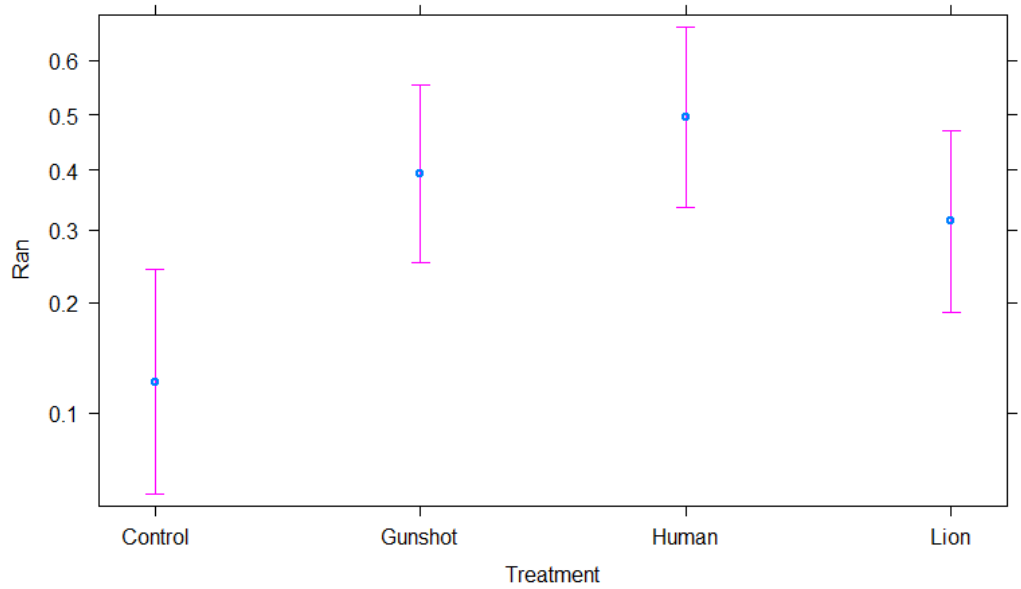

Figure 5. Probability of rhinos to run after the playback and 95% confident limits for each playback treatment for GLMM analysis.

3.3. Response 2: Defensive Behaviour

3.3.1. GLM

The probability of rhinos exhibiting a defensive response or not was best explained by the simplest model i.e. model 4 including only the single term for playback treatment. Both gunshot and lion treatments resulted in a higher probability of displaying defensive behaviour relative to the control treatment (table 6). The response to the human voice treatment did not differ from the control.

Table 6. Estimate value, standard error, z and p value for each explanatory variable from the best model explaining the probability of rhinos responding defensively to playback disturbance. Model structures and AIC support for all competing GLM models is shown below the estimates table with the selected model highlighted in grey.

	Estimate	**Std. Error**	**z value**	**Pr(>|z|)**
Intercept	-2.04	0.43	-4.69	<0.001 ***
Playback Gunshot	1.13	0.53	2.13	0.033 *
Playback Human	0.67	0.55	1.23	0.221
Playback Lion	1.31	0.52	2.50	0.012 *

	Model structure	AIC
Model 1	PI (c/f)+Treatment+ GS+ PI(c/f) x Treatment+ Treatment x GS	236.97
Model 2	PI (c/f) +Treatment+ GS+ PI(c/f) x Treatment	233.06
Model 3	PI (c/f) +Treatment+ GS+ Treatment x GS	234.52
Model 4	**Treatment**	227.99

Figure 6 shows that rhinos have a higher expected probability to exhibit defensive behaviour for lion vocalizations and gunshot treatments compared to control sounds.

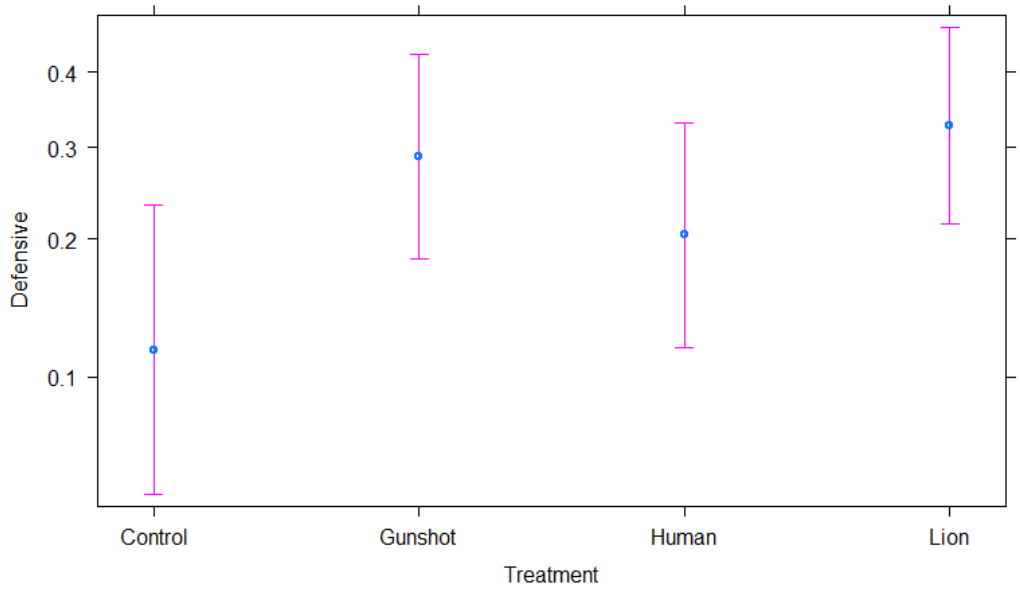

Figure 6. Probability of rhinos to be defensive or not and 95% confident limits for each playback treatment for GLM analysis.

3.3.2. GLMM

The probability of rhino exhibiting a defensive response was best explained again by model 4 that contained only the single term for playback treatments (table 7). Similar to the GLM result, rhinos were more likely to react defensively against gunshot and lion vocalizations compared to control sounds (figure 7).

Table 7. Estimate value, standard error, z and p value for each explanatory variable from the best model explaining the probability of rhinos responding defensively from playback disturbance. Model structures and AIC support for all competing GLMM models is shown below the estimates table with the selected model highlighted in grey.

	Estimate	**Std. Error**	**z value**	**Pr(>|z|)**
Intercept	-2.47	0.40	-6.20	<0.001 ***
Playback Gunshot	1.05	0.43	2.48	0.013 *
Playback Human	0.51	0.46	1.11	0.269
Playback Lion	1.37	0.44	3.12	0.002 **

	Model structure	AIC
Model 1	PI (c/f)+Treatment+ GS+ PI(c/f) x Treatment+ Treatment x GS	527.17
Model 2	PI (c/f) +Treatment+ GS+ PI(c/f) x Treatment	523.71
Model 3	PI (c/f) +Treatment+ GS+ Treatment x GS	522.54
Model 4	**Treatment**	515.37

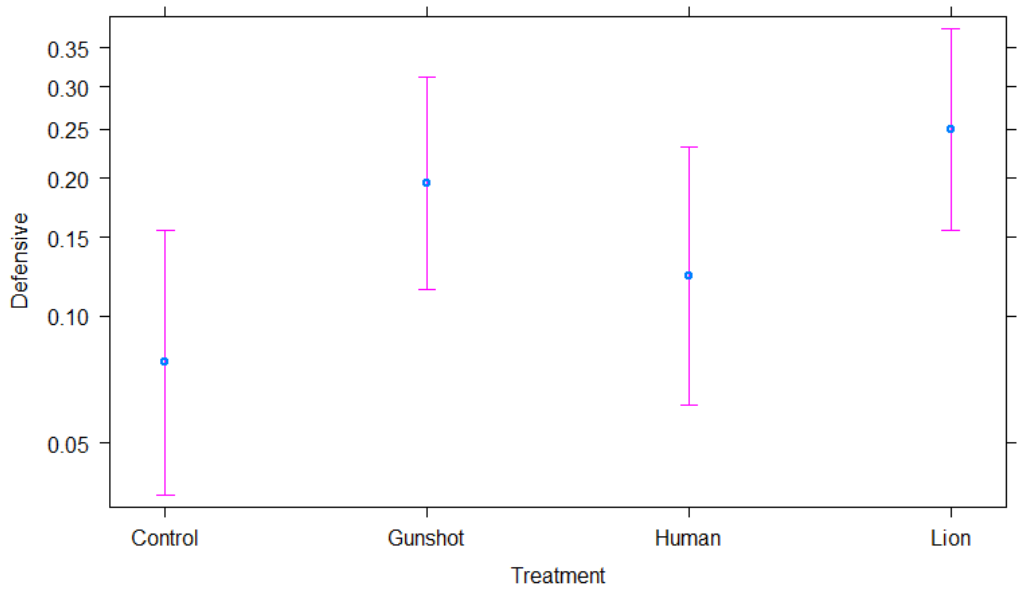

Figure 7. Probability of rhinos to exhibit defensive responses after the playback and 95% confident limits for each playback treatment for GLMM analysis.

3.4. Response 3: Low vigilance vs high vigilance

Most of the rhinos reached a high state of vigilance at least one time within a sequence. In the first exposures (GLM), 90.60% of the rhinos were high vigilant and for all the sequences (GLMM), 79.25% reached high vigilance state.

3.4.1. GLM

In this case, three models were equally supported, models 2 and 3 i.e. models with one interaction term each, and the model 4, i.e. the model with only playback treatment as variable, which I selected for its parsimony (table 8).

The probability of rhinos displaying high vigilance increased for lion vocalizations compared to the baseline level of rhino vigilance during control sound playbacks (table 8). The response to both human-associated sounds was not different from the controls.

Table 8. Estimate value, standard error, z and p value for each explanatory variable from the best model explaining the probability of rhinos being low or high vigilant for playback disturbance. Model structures and AIC support for all competing GLM models is shown below the estimates table with the selected model highlighted in grey.

	Estimate	**Std. Error**	**z value**	**Pr(>|z|)**
Intercept	1.06	0.41	2.57	0.010 *
Playback Gunshot	1.02	0.67	1.53	0.127
Playback Human	18.51	1659.38	0.01	0.991
Playback Lion	1.89	0.83	2.27	0.024 *

	Model structure	AIC
Model 1	PI (c/f)+Treatment+ GS+ PI(c/f) x Treatment+ Treatment x GS	89.06
Model 2	PI (c/f) +Treatment+ GS+ PI(c/f) x Treatment	85.60
Model 3	PI (c/f) +Treatment+ GS+ Treatment x GS	84.46
Model 4	**Treatment**	84.40

3.4.2. GLMM

The same three models were equally supported in the GLMM analysis. Models 2 and 3 i.e. models including one interaction term, and model 4 i.e. the model including the single term for the playback treatment. Compared to the baseline level of rhino vigilance during control sound playbacks, only lion vocalizations and human voices playbacks triggered a significant increase in the probability of rhino being highly vigilant (table 9).

Table 9. Estimate value, standard error, z and p value for each explanatory variable from the best model explaining the probability of rhinos being low or high vigilant for playback disturbance. Model structures and AIC support for all competing GLMM models is shown below the estimates table with the selected model highlighted in grey.

	Estimate	**Std. Error**	**z value**	**Pr(>|z|)**
Intercept	0.94	0.33	2.86	0.004 **
Playback Gunshot	0.29	0.41	0.70	0.483
Playback Human	1.09	0.47	2.32	0.021 *
Playback Lion	1.32	0.47	2.84	0.004 **

	Model structure	AIC
Model 1	PI (c/f)+Treatment+ GS+ PI(c/f) x Treatment+ Treatment x GS	405.72
Model 2	PI (c/f) +Treatment+ GS+ PI(c/f) x Treatment	403.14
Model 3	PI (c/f) +Treatment+ GS+ Treatment x GS	402.13
Model 4	**Treatment**	401.92

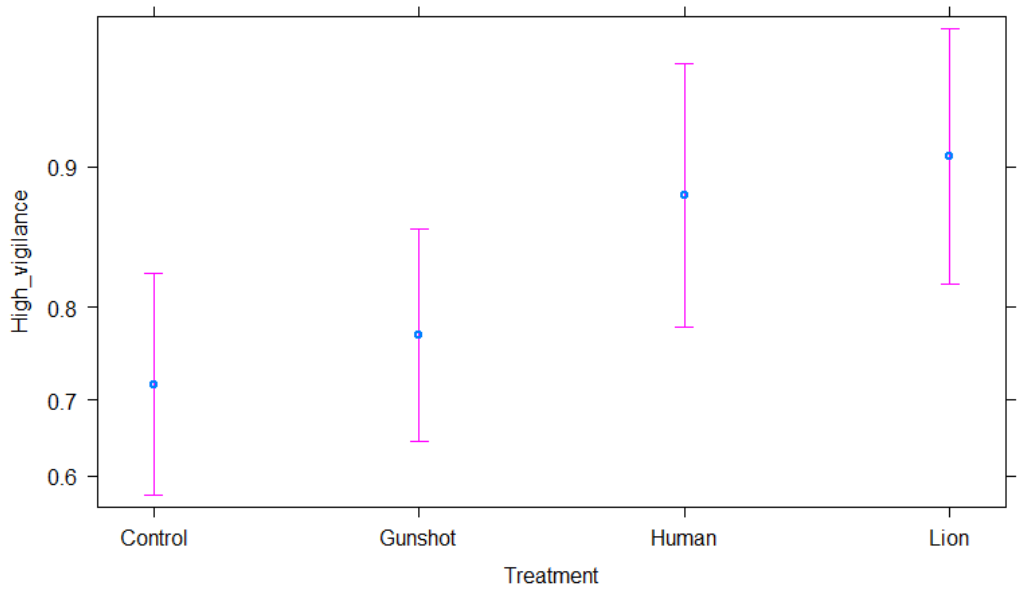

Figure 8. Probability of rhinos to being high vigilant after the playback and 95% confident limits for each playback treatment for GLMM analysis.

3.5. Response 4: Scanning

3.5.1. GLM

The proportion of time rhinos were scanning was best explained by the model with only playback treatment. However, the model did not support any difference in rhinos' response to the treatments (table 10).

Table 10. Estimate value, standard error, z and p value for each explanatory variable from the best model explaining the average proportion of time of rhinos scanning for playback disturbance. Model structures and AIC support for all competing GLM models is shown below the estimates table with the selected model highlighted in grey

	Estimate	**Std. Error**	**z value**	**Pr(>|z|)**
Intercept	0.08	0.01	7.63	<0.001 ***
Playback Gunshot	0.01	0.02	0.62	0.53
Playback Human	-0.03	0.02	-1.65	0.10
Playback Lion	-0.01	0.02	-0.63	0.53

	Model structure	AIC
Model 1	PI (c/f)+Treatment+ GS+ PI(c/f) x Treatment+ Treatment x GS	-460.48
Model 2	PI (c/f) +Treatment+ GS+ PI(c/f) x Treatment	-462.84
Model 3	PI (c/f) +Treatment+ GS+ Treatment x GS	-462.36
Model 4	**Treatment**	-464.46

3.5.2. GLMM

Again, the proportion of time rhino spent scanning was best explained by playback treatment effects. I correct heteroscedasticity across treatments. Among risky treatments only human voices returned a p-value<0.1 (table 11).

Table 11. Estimate value, standard error, t and p value for each explanatory variable from the best model explaining the average proportion of time of rhinos spent scanning for playback disturbance. Model structures and AIC support for all competing GLMM models is shown below the estimates table with the selected model highlighted in grey

	Estimate	**Std. Error**	**t value**	**p-value**
Intercept	0.07	0.01	8.19	<0.001 ***
Playback Gunshot	-0.01	0.01	-0.47	0.640
Playback Human	-0.02	0.01	-1.78	0.075 .
Playback Lion	-0.002	0.01	-0.22	0.823
	Model structure			AIC
Model 1	PI (c/f)+Treatment+ GS+ PI(c/f) x Treatment+ Treatment x GS			-1180.93
Model 2	PI (c/f) +Treatment+ GS+ PI(c/f) x Treatment			-1205.91
Model 3	PI (c/f) +Treatment+ GS+ Treatment x GS			-1211.64
Model 4	**Treatment**			-1247.91

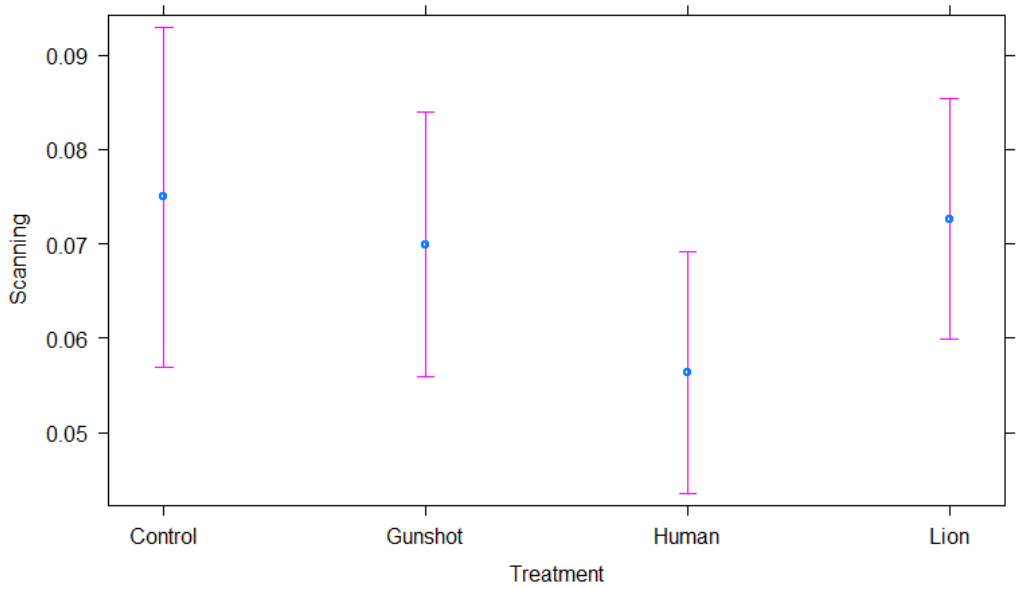

Figure 9. Average proportion of time rhinos spent scanning and 95% confident limits for playback each treatment for GLMM analysis.

3.6. Response 5: Sequence length

3.6.1. GLM

Sequence length was best explained by the full model i.e. model 1 including the additive effects of the playback treatments, group size and poaching intensity (measured as a continuous variable over a two km radius and a two year period) and the two interaction terms (table 12).

When only exposed to control sounds, rhinos' length of stay decreased as poaching intensity increased. Yet, when exposed to human voices and lion vocalizations, rhinos' length of stay increased with poaching intensity (figure 10). Sequence length did not change with poaching intensity for gunshots. In addition, when exposed to control sounds and human voices, rhinos stayed at latrines for longer when they were in larger groups. Yet, when exposed to gunshot sounds and lion vocalizations, they no longer increased their length of stay when in larger groups (figure 10).

Table 12. Estimate value, standard error, z and p value for each explanatory variable from the best model explaining sequence length for playback disturbance. PI_(2k2y) indicates a Poaching index calculated over 2 years and a 2 km radius. Model structures and AIC support for all competing GLM models is shown below the estimates table with the selected model highlighted in grey.

	Estimate	**Std. Error**	**z value**	**Pr(>|z|)**
Intercept	0.06	0.89	0.06	0.950
PI_(2k2y)	-0.17	0.08	-1.95	0.052 .
Playback Gunshot	1.80	1.30	1.39	0.167
Playback Human	-2.21	1.38	-1.60	0.111
Playback Lion	0.79	1.32	0.60	0.551
Group size	2.52	0.50	5.01	<0.001 ***
PI_(2k2y): Gunshot	0.21	0.12	1.76	0.079 .
PI_(2k2y): Human	0.36	0.12	2.93	0.004 **
PI_(2k2y): Lion	0.32	0.13	2.50	0.013 *
Gunshot: Group size	-2.58	0.73	-3.55	<0.001 ***
Human: Group size	-0.49	0.72	-0.68	0.498
Lion: Group size	-2.22	0.69	-3.23	0.001 **

	Model structure	AIC
Model 1	PI (c) +Treatment+ GS+ PI (c) x Treatment + Treatment x GS	1012.97
Model 2	PI (c) +Treatment+ GS+ PI (c) x Treatment	1026.24
Model 3	PI (c) +Treatment+ GS+ Treatment x GS	1017.35
Model 4	Treatment	1042.60

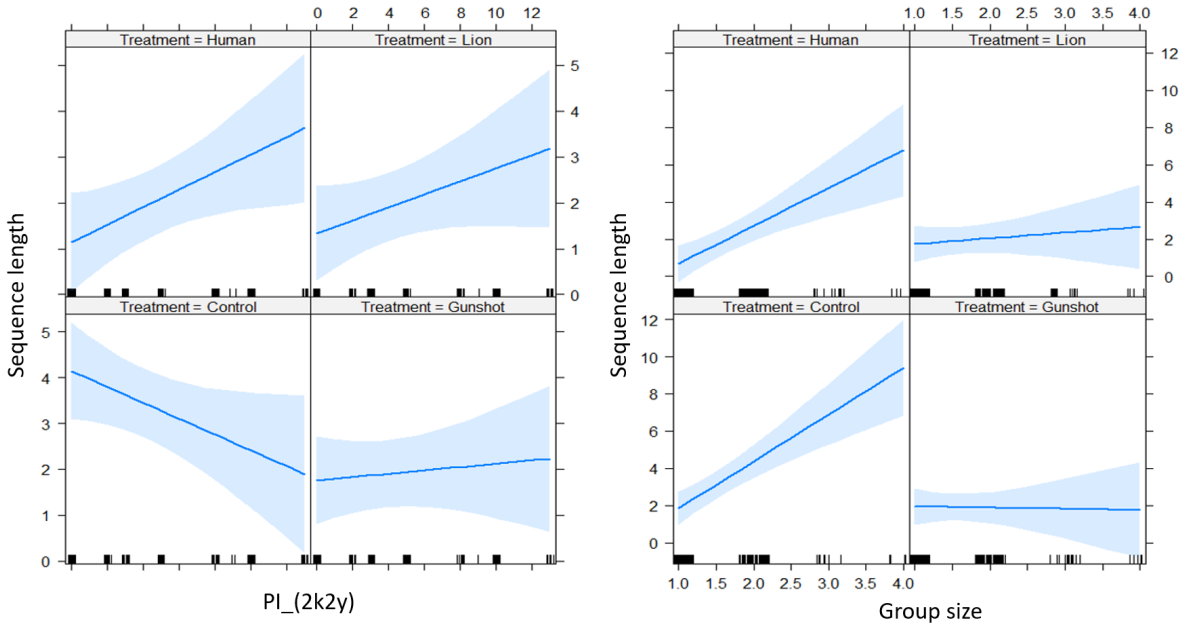

Figure 10. Sequence length depending on the interaction effects of playback treatments and Poaching Index (PI_(2k2y) calculated over 2 km radius and 2 years) and interaction effects of group size and playback treatments for GLM analysis. Poaching index values have been removed at the request of the park management for security reasons.

3.6.2. GLMM

In contrast to the GLM results, the GLMM output showed sequence length to be best explained by model 3 i.e. model including additive effects of the playback treatments, group size and poaching intensity (measured as a continuous variable over a one km radius and a two year period) and the interaction between treatment and group size (table 13). In these models, I corrected heteroscedasticity across playback treatments.

When exposed to control sounds and human voices, rhinos stayed at latrines for longer when they were in larger groups. Yet, sequence length did not differ with group size when exposed to gunshot sounds and lion vocalizations (figure 11).

Table 13. Estimate value, standard error, degrees of freedom (DF), t and p value for each explanatory variable from the best model explaining sequence length for playback disturbance. PI_(1k2y) indicates a Poaching index calculated over 1 km radius and a 2 years. Model structures and AIC support for all competing GLMM models is shown below the estimates table with the selected model highlighted in grey.

	Estimate	Std. Error	DF	t value	p-value
Intercept	-0.55	1.00	149	-0.55	0.581
PI_(1k2y)	0.06	0.05	17	1.38	0.185
Playback Gunshot	2.24	1.07	104	2.10	0.038 *
Playback Human	0.20	1.34	104	0.15	0.883
Playback Lion	2.54	1.10	104	2.31	0.023 *
Group Size	2.18	0.58	104	3.78	<0.001 ***
Gunshot: Group Size	-2.23	0.61	104	-3.68	<0.001 ***
Human: Group Size	-0.86	0.75	104	-1.15	0.2547
Lion: Group Size	-2.19	0.62	104	-3.51	<0.001 ***

	Model structure	AIC
Model 1	PI (c) +Treatment+ GS+ PI (c)x Treatment + Treatment x GS	1251.21
Model 2	PI (c) +Treatment+ GS+ PI (c) x Treatment	1267.15
Model 3	PI (c) +Treatment+ GS+ Treatment x GS	1247.62
Model 4	Treatment	1254.77

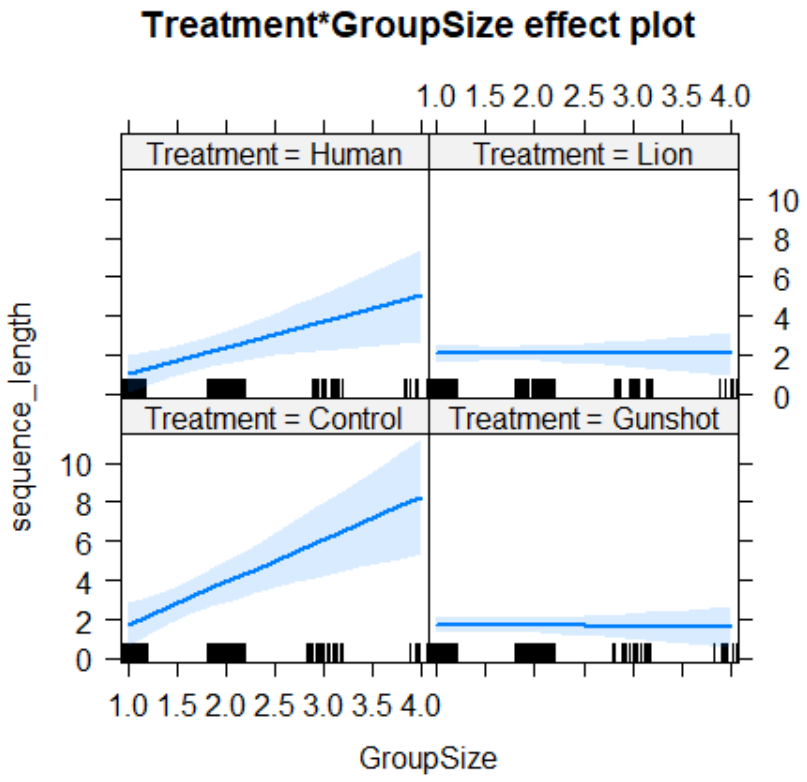

Figure 11. Sequence length for each treatment depending on their group size for GLMM analysis.

4. Discussion

Rhinos were more likely to run for risky treatments than for control sounds. They also were more likely to respond defensively from gunshots and lion treatments compared to control treatments. In addition, there was a higher probability that they reached a high vigilance state for lion vocalizations than for control sounds. In contrast, rhinos spent the same time scanning for control sounds and risky treatments. Group size did not influence the strength of the responses for the first four variables. Moreover, rhinos stayed at the latrine for a similar amount of time regardless of group size, when they were exposed to gunshots and lion vocalizations. Following control sounds, rhinos spent less time on latrines in areas with higher poaching intensity. However, in contrast to what I expected, rhinos stayed longer at latrines as poaching intensity increased when they were exposed to human voices and lion vocalizations.

4.1. Strength of the responses to control vs risky treatments.

Rhinos ran more often for all simulated risk treatments than for the sounds of birds. However, this only became clear when I was able to consider more videos following exposure to the sound (as was allowed during GLMM analyses). When I was restricted to only using the videos shortly following the sound disturbance (the restriction in the GLM analysis), rhinos did not appear to run more from lion vocalizations. These results are partially consistent with the results found by Zanette and Clinchy, (in press). In both studies the probability of rhinos running was higher when exposed to human voices compared to control sounds. In contrast to their results, however, I also found rhinos responded more strongly to the sounds of gunshots than the sounds of birds. Running from a stimulus is a clear fear response. The fact that rhinos ran from gunshot sounds shows a clear non-ambiguous response of rhinos to human associated disturbance or even to human predation pressure.

In a previous study, rhinos ran from repeated unpleasant mechanic noise (siren) (Penny et al., 2019). It is unlikely that rhinos in HiP ran due to gunshots sounds' loudness because the volume was the same across all treatments, but they may ran from gunshots sounds because it is a relatively novel sound for them. However, this would not explain why rhinos did not run from gunshots sounds in other areas (Zanette and Clinchy, in press).

There was a higher probability of defensive responses to gunshots and lion vocalizations treatments compared to control sounds in both analyses, however, I did not find rhinos to increase their defensive behaviour when exposed to human voices. In contrast to running, defensive responses are more difficult to score in rhinos. I could have interpreted behaviours as defensive that may not have been defensive or even missed some defensive behaviours, for example, when a mother tries to protect her calf by putting herself between the speaker and the calf. A less clear response of rhinos to human voices could be due to defensive behaviours that were misinterpreted.

Regarding vigilance state, rhinos were more vigilant when exposed to human voices although this only became clear when we were able to consider all sequence responses (in the GLMM analyses). When I was restricted to only first exposures (the restriction in the GLM analysis) rhinos did not appear to be more vigilant in response to human voices, only to lion vocalizations. However, it is surprising that rhinos did not increase their vigilance in response to gunshots. This could be due to methodological procedures. Most of the rhinos reached high vigilance state at least once during a sequence, which led to a large disproportion of high vigilant rhinos. Perhaps, it could be better to test the average amount of time that the rhinos spent low or high vigilant for each treatment, or instead of using only low vigilance, include no vigilance as well, with behaviours such as wallowing (see table 1).

It is important to discuss the influence of tourism in these responses. In HiP, due to tourists, rhinos did not always experience human voices as a threatening sound. This could be the cause of why rhinos did not respond defensively to human voices, but they defended against clear dangerous sounds such as gunshots. In the same way, the influence of tourism may explain that rhinos were vigilant from human voices only after repeated exposures. A continuous exposure to non-threatening human voices could make it more difficult for them to associate human voices with poachers. A further analysis including distance to tourist roads or human settlements in the park, would be useful for determining the influence of tourism on rhinos behavioural responses. However, rhinos effectively ran from both gunshots and human voices, which mean fear response to those stimuli. This response, running, was lower, compared to control sounds, when exposed to lion

vocalizations. It is important to say that a higher probability of running for any of these playback treatments compared to control sounds would potentially explain a decrease of defensive and vigilance responses to the same stimuli. In addition, this could suggest a response selection process, where the rhinos differentiate among various stimuli and respond according to risk perceived. Lions would only represent a potential threat to rhino calves, but not to adults. In contrast, humans could be perceived as threat by adult rhinos as well. In this context, it would make sense that rhinos increase vigilance or defend themselves or their calves against lions and they flee from a predator where defence may be a less successful strategy.

Scanning did not differ among playback treatments. This could be because scanning is a common behaviour that rhinos continuously do and they might increase its frequency with all sounds and not particularly for simulated risk ones.

Group size influence

In relation to the influence of group size on anti-predator responses, I found that rhinos stayed longer with larger group size for control and human voices. Additionally, rhinos remained around the same amount of time for gunshots and lion vocalizations despite of group size (figures 9 and 10). These results could make sense as a large group behaviour. In larger groups the probability that one individual flee from human voices would potentially decrease simply because it feels safer within the group. This could also reinforce the aforementioned theory that rhinos could not always perceive human voices as a threatening sound. In that case, a larger group of rhinos would stay longer when they hear non-threatening sounds, such as human voices or bird sounds. In contrast, for always threatening sounds, such as gunshots or lions, rhinos would prefer to leave the latrine before standing against repeated threatening sounds. Also, because rhinos were exposed in latrines, the time spent in front of the camera and socialising could work as a trade-off. When rhinos were exposed to not always threatening sounds, they opted for socialising. When exposed to clear threatening sounds they instead left the latrine. However, rhinos also showed defensive response against gunshots and lion vocalizations. This could be because they exhibit a defensive response on the very first time they heard that sound, but they eventually left the place after hearing them twice. This would also match with a sequence length of two videos (figures 9 and 10).

A previous study with other African ungulate species, showed a trade-off between group size and vigilance (Creel et al., 2014). The results in this study did not show group size-vigilance trade-off. This could be because of the high proportion of rhinos that reached the high level of vigilance within a sequence at least once (i.e. 90.6% for first exposures and 79.25% for all the sequences). However, this high proportion of rhinos being highly vigilant is consistent with the

results found by Creel et al., (2014), where species with smaller group sizes (compared to species with larger herds, e.g. impala or zebra) had higher levels of vigilance.

Strength of responses with poaching intensity

Contrary to what I expected, the probability of rhinos running for human associated treatments did not increase with poaching intensity. In addition, defensive responses also did not depend on poaching risk perceived. This could also be linked to response selection (see above), if rhinos were more likely to exhibit defensive behaviour for lion vocalizations, poaching intensity might not influence defensive response because PI is calculated as risk perceived from human predation pressure, not lion. In contrast to the results in other species (Creel et al., 2014), the probability of rhinos being highly vigilant did not increase with predation risk. This could be due to the large percentage of rhinos that were highly vigilant (see previous paragraph) which would make it difficult to see changes in vigilance between high and low poaching intensity areas. Moreover, rhinos were always highly vigilant from human voices treatment, regardless of poaching intensity. Finally, rhinos stayed more time for human voices and lion vocalizations when poaching intensity increased.

These results suggest that rhinos are exhibiting anti-predator responses to renewed human predation pressure, e.g. running from human associated sounds. However, these responses did not increase their strength with poaching intensity in the area. Due to uniformity of the responses across the landscape, it is uncertain if these responses were a result of an evolutionary or learning process or a combination of the two. If they had only respond to human associated sounds in high poaching intensity areas, it would suggest a recently acquired behaviour. This lack of variation in responses strength through the landscape could be due to limited spatial territory. In a 900 km^2 park, a rhino may be using low and high poaching intensity areas equally. This could potentially explain the different responses to gunshots sounds in Kruger (Zanette and Clinchy, in press) and in this study. In a larger area (Kruger) rhinos' territories might not be occupying low and high poaching intensity areas at the same time. Additionally, poaching intensity changed rapidly for each area. In the three years period that I used for estimating PI, some areas that were a poaching hotspot one year, were not the year after and vice versa. In this context, rhinos would be reacting as naïve preys (Berger et al., 2001) to poaching activity. Furthermore, naïve rhinos of low poaching intensity areas could occupy the territories of killed rhinos in high poaching intensity areas. Because of the high efficiency of human hunters (Ripple et al., 2016), naïve rhinos would potentially not have the opportunity to incorporate information about their new predator. However, it is important to mention that animals which live in herds, such as rhinos

should have a higher chance to learn that gunshots sounds are associated to risk. In future studies, it may be useful to include another control treatment that sounds "similar" to gunshots, such as thunder. This could help to identify if rhinos' responses are learnt behaviours specific to gunshots, or on the contrary they are evolved behaviours for unexpected sounds.

Finally, it is important to mention that in most of the models where PI was significant, it was measured using 3 or 2 km and 3 or 2 years period (appendix A). Therefore I determine that the range of illegal killing events that I used to calculate PI was not restrictive to represent poaching intensity in the sampling areas.

4.2. Application of results for management practice

This novel understanding of rhino responses to threat stimuli could be useful from a management perspective. There is a general consensus that the actual anti-poaching efforts have been relatively successful (Knight, 2012). However, some studies are sceptic about the sustainability of current strategies. This scepticism is based partly on an oversimplified view of the poaching network and the continued role that socio-economic inequality is likely to play in maintaining poaching pressure (Duffy et al., 2014), while others highlight the socio-economic costs of anti-poaching militarisation. (Annecke and Masubelele, 2016). Critical voices call for additional new mechanisms to tackle illegal wildlife trafficking (Ripple et al., 2015, Duffy et al., 2015, Massé, 2019). Some of these proposed alternative mechanisms focus on human society (*e.g.* Hübschle and Shearing, 2018) or legislative solutions (*e.g.* Biggs et al., 2013), while others are based on conservation management strategies (*e.g.* Penny et al., 2019). In this context, comprehending how rhinos are adapting or not adapting to "poaching predation pressure" could help to develop new anti-poaching strategies. These strategies aim to elicit a rhino behavioural response to reduce exposure to risky situations, such as avoidance of certain areas with high poaching rates. As an example, the results of the study could help to transform the risk of poachers perceived by rhinos into a management tool for rhino conservation. This "management/hunting for fear" approach could consist of creating a landscape with spatially predictable and temporally unpredictable risk cues (Cromsigt et al., 2013). For rhinos, this management tool could be implemented in a non-lethal way to try to manipulate their movement and behaviour to make them less vulnerable. This would have side effects on vegetation structure due to rhinos' impact on among other ecosystem properties, the maintenance of grazing lawns and short grass proportion (Cromsigt and te Beest, 2014). In addition, this rhino behavioural change could affect how they contribute to homogenising nutrient distribution across a landscape of fear (Le Roux et al., 2018). These changes in vegetation heterogeneity and nutrient distribution might influence

herbivore diversity and facilitate habitat fragmentation (Cromsigt, Prins and Olff, 2009). In conclusion, potential management actions to protect rhinos against poaching must take into account possible impacts on the ecosystem. However, before developing new management mechanisms it is necessary to have a better understanding of how altered rhino behaviours and habitat use would influence ecosystem structure and function.

5. Conclusions

Despite rhinos showing anti-predatory responses to poaching stimuli, these responses were not particularly strong in the areas where they were most needed. If naïve rhinos do not perceive poaching risk, they will not avoid high risky areas, and will be more vulnerable. Nevertheless, rhinos selected risk-appropriate anti-predator responses depending on the predator risk. On the one hand, defensive behaviours were more common against wild top-predator which did not represent a potential threat to adult rhinos. On the other hand, rhinos preferred to run away from human risk, which probably would be the most effective response to avoid a poacher. However, rhinos responded by both running and acting defensively to gunshots. In addition, group size had no influence on rhino behaviour for gunshot and lion perceived risk, but it increased rhino confidence against human voices. Unfortunately, this information could not be used immediately to develop new anti-poaching mechanisms. Further knowledge on altered rhino behaviours and habitat use would be necessary to implement successful anti-poaching strategies that would not alter ecosystem functions.

6. Acknowledgements

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8. Appendix

Appendix A. PI scores and their p-value significant levels for each response variable and analysis.

*Table A. PI scores for each model when they were significant. Grey boxes for analyses were PI p-value was not significant for any model. P-values for each treatment being <0.001***, <0.01**, <0.05 * and <0.1•.*

	Ran	Defensive	Vigilance	Scanning	Sequence length
GLM	2nd best model: PI_(3 km 2 years)*		2nd best model: PI_(2 km 3 years)*		Best model: PI_(2 km 2 years)•
GLMM			2nd best model: PI_(2 km 3 years)•	2nd best model: PI_(3 km 3 years)*	

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